COPROLITES OF *PTILOPHYLLUM* CUTICLES FROM THE MIDDLE JURASSIC OF NORTH YORKSHIRE

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ABSTRACT

Large coprolites from the Roseberry Topping plant bed (Middle Jurassic) consist mainly of *Ptilophyllum* fragments. Their significance is discussed.

DESCRIPTION

THE SPECIMENS discussed here were collected over 50 years ago by Dr H. Hamshaw Thomas, though so far as I know he never described them. They were found in siltstones of Lower Deltaic age which form the upper layers of the Roseberry Topping plant bed (Thomas 1913). Besides being much the largest of the half dozen or so coprolites now known from the Yorkshire Middle Jurassic they have yielded an entirely different flora from those previously investigated.

The material is in the Collection of the Palaeontology Dept. of the British Museum (Natural History), and consists of six blocks labelled V 58510 and an additional one labelled V 58510a. Those labelled V 58510 look as if they once formed part of a single larger block which broke up in collecting, and judged on the six fragments this original block must have been large, having more than 250 pellets covering an area of about 1 m^2. As the pellets occur on several bedding planes, occupying about 5 mm thickness of the cross-bedded matrix, I assume that their burial was rapid. Otherwise I would expect them to have become widely dispersed, whereas they are in fact somewhat clustered into random groups, very like fresh droppings of a modern herbivore such as a rabbit. Indeed, much like freshly dropped rabbit pellets the round or oval outlines of the fossil ones sometimes show a constriction to a point on the side from which they were extruded, and fine striations, presumably caused by the anal sphincter, may be seen radiating from this point onto the impression surfaces. The clarity of these markings in the fossil doubtless indicates that the fresh pellets were of a firm consistency and also of a uniform, possibly gelatinous, texture.

The diameter of the pellets ranges from 8 to 18 mm, though they are mostly 10–13 mm. Where present the substance, which is composed of compressed cuticle fragments and finely divided organic detritus, is a dull black colour. It is about 0·5 mm thick, thinning to the edges, and the lack of compression border suggests that the pellets were perhaps somewhat flattened before their final burial (compression theory of Walton 1936). The fact that adjacent pellets sometimes overlap one another may equally indicate that they were originally rather flattened (Harris

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FIG. 3. Coprolite, chiefly of *Ptilophyllum pectinoides* (Phillips) Phillips, from Roseberry Topping, north Yorkshire. V 58510, × 1. Drawn on a photograph.

1946). However they could well overlap if, as in the pelleted form of sheep dung, they were sometimes produced adhering together in masses.

V 58510a may have come from a different horizon of the Roseberry Topping siltstone as the colour of the matrix is rather darker. The pellets have a similar form to those of V 58510 but they are uniformly smaller, about half the size, and many more of them overlap their neighbours. As, however, they yield an almost identical flora to those of V 58510 I imagine that they may well have been produced by the same kind of animal, but possibly an individual having a smaller anus ; by analogy a young rabbit produces much smaller pellets than a fully grown one.

Of the abundant cuticles yielded by Schulze-Ammonia maceration over 99% of the determinable ones are fragments from leaves and petioles of *Ptilophyllum pectinoides* (Phillips) Phillips. Only a few scraps from other species were seen, chiefly a specifically indeterminable *Solenites* or *Czekanowskia* and a Bennettitalean cuticle resembling *Nilssoniopteris vittata* (Brongn.) Florin (though possibly also referable to certain species of *Anomozamites* or *Pterophyllum*). There are in addition several well-preserved micropylar and interseminal scale cuticles identical with those of *Williamsonia hildae* Harris and *W. leckenbyi* Nathorst.

The size of the cuticle fragments reaches about 1 mm × 3 mm, though it is usually 1 mm^2 or smaller. The substance of the pellets, however, shows marked fracturing into rectangular blocks and this, which presumably occurred after deposition, may well have reduced the size of some of the cuticle fragments.

DISCUSSION

Coprolites from the Yorkshire Deltaic beds are rare and informative fossils. Other than occasional insects, fish skeletons and reptilian footprints they provide the only evidence so far known for the activity of vertebrate animals in the delta. The examples previously described, collected from the Gristhorpe Bed and at Beast Cliff, have been discussed by Harris (1946, 1951, 1956, 1964) and Harris *et al.* (1974). None of them, however, has pellets even as much as half the size of those in the present specimens and they have yielded entirely different floras, chiefly composed of comparatively delicate leaf and seed cuticles or pollen : mainly *Caytonia*, *Solenites*, *Androstrobus*, and thin Bennettitalean cuticles. In contrast to these the leaf of the Roseberry specimens, *Ptilophyllum pectinoides*, had a robust cuticle. Frequently also this leaf was resinous, as is indicated both in hand specimens and in the coprolite by the internal casts of mesophyll cells sometimes seen adhering in patches to the upper cuticle (Pl. 3, figs 1, 2, 3 ; Harris 1949). I conclude that the Roseberry herbivore was a rather larger animal than those which provided Harris's specimens, perhaps the size of a sheep or large rabbit. Indeed the present pellets are remarkably similar to the pelleted form of sheep's dung. The animal clearly could utilize the rather harsh resinous leaves of *Ptilophyllum*, though it did not digest the resin to any noticeable extent.

The nature of the herbivore is, of course, unknown, though presumably it was a reptile, such as an ornithopod dinosaur, or possibly a mammal. If a mammal then the pellets seem larger than would be expected from any mammals of Middle

Jurassic age so far described in the literature. Gut dimensions, however, though generally related to size, do not display a direct mathematical proportionality to it, and the analogy to the size of a sheep is approximate.

The intimate association, within the coprolite, of the flower *Williamsonia* with the leaf *Ptilophyllum* is striking. These organs are also seen associated together as hand specimens in the normal flora at Roseberry and on this basis, with additional evidence from morphologically intermediate organs, Harris (1969) has attributed them to the same plant. In this respect it seems that the coprolite provides a remarkably faithful representation of the normal Roseberry flora. Assuming that the animal fed on living plants the evidence thus reinforces Harris's restoration.

The overall floristic composition of the dung is also like that of the normal flora at certain layers in the upper part of the siltstone, and this is interesting in view of the complex factors, such as fragmentation and sorting, which normally operate during the deposition, as at Roseberry, of terrestrial plants in stream channel deposits. As it is natural to assume that the herbivore fed on living vegetation the facts suggest that the fragmentary debris which constitutes the normal fossil flora might sometimes be a remarkably straightforward representation of plant communities then growing in the vicinity. They may also indicate that the plants grew fairly close to Roseberry, for if the animal had strayed far one might expect the dung to yield at least a few species not normally found there.

There is, however, a simpler explanation. The animal may possibly have been a scavenger, browsing on the *Ptilophyllum* debris which was being transported in the deltaic streams and ultimately deposited in great abundance at Roseberry and other localities. If this is right the dung would be expected to show fragments of species we already know from the normal Roseberry flora, but it would not necessarily indicate anything about plant communities in the living vegetation other than that their debris could be palatable to an unknown animal.

Unfortunately there is insufficient evidence to make a certain choice between these explanations, though so far as I know there are no modern vertebrates which would normally prefer a diet of rotting leaves to fresh ones. For this reason the first explanation seems perhaps nearer the truth.

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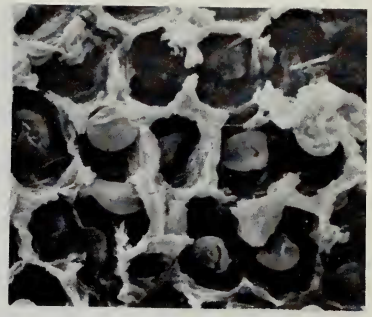
PLATE 3

Ptilophyllum pectinoides (Phillips) Phillips

FIGS 1, 2, 3. Upper cuticle prepared by Schulze maceration of a hand specimen found at Hasty Bank. Fig. 1, V 58591, light micrograph, × 160. Fig. 2, inner surface of cuticle; scanning electron micrograph showing resinous casts inside the 'cutinized' walls of palisade mesophyll cells, × 336. Fig. 3, same, × 1040.

FIG. 4. Coprolite, chiefly of *Ptilophyllum pectinoides*, from Roseberry Topping. V 58510, × 1. Photo: J. V. Brown.

1



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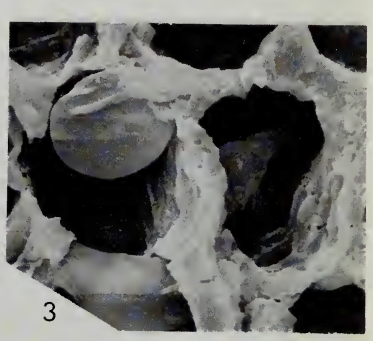

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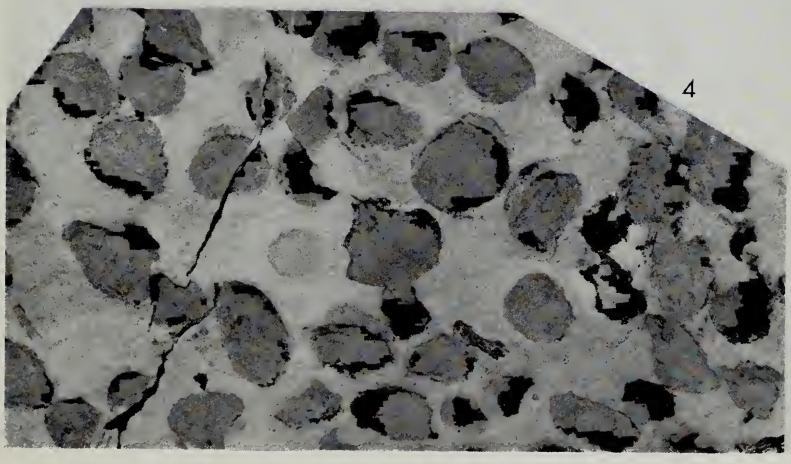

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